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ORIGINAL RESEARCH ARTICLE

Effects of retained node numbers on berry maturity and yield components of cane-pruned Sauvignon blanc

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ABSTRACT

Cane pruning is used in most New Zealand Sauvignon blanc vineyards to manage yield, vine balance (relationship between vegetative growth and fruit growth) and fruit primary and secondary metabolites. The source–sink ratio (TLA/FM—total leaf area to fruit mass or ELA/FM—exposed leaf area to fruit mass), the fruit mass to pruning mass (FM/PM), the fruit mass to cane mass (FM/CM) and fruit composition provide an assessment of the vine performance and balance. The interpretation of these metrics (i.e., TLA/FM, ELA/FM, FM/PM, FM/CM) requires their comparison with known optimal ranges specific to cultivars, locations and growing conditions. More often, such context- and cultivar-specific optimal ranges do not exist, thus warranting research to investigate them. To understand the influence of retained node numbers on the vegetative and fruit development of Sauvignon blanc, grapevines were pruned across three vineyard sites (two in Marlborough—Site 1 and 2, and one in Waipara—Site 3) over two growing seasons, retaining 10, 20, 30, 40 and 50 nodes on one to four canes (each cane carrying ten nodes, with 50-node vines carrying on average 12.5 nodes on each of the four canes). The accumulation of soluble solids (TSS) generally increased at lower node numbers and vine yields, reflecting an increase in ELA/FM, with 50-node vines having the least TSS concentration at harvest. The average berry mass, titrable acidity (TA) and pH were unaffected by node numbers over the two seasons. A low source–sink ratio induced by high node numbers not only reduced the vine capacity to ripen the current crop but also reduced the following season's bunch number per shoot (from 1.8 to 1.6 bunches per shoot; $p < 0.05$), average bunch mass (from 82.0 ± 6 g to 67.7 ± 3 g; $p < 0.01$) and bunch mass per shoot (from 153.5 ± 15 g to 106.7 ± 9 g; $p < 0.05$). When compared to 50-node vines, 10-node vines had a two-fold increase in the average cane mass (from 30.1 ± 3.9 g to 69.2 ± 8.7 g; $p < 0.001$) and average old cane mass (from 82.4 ± 6.9 g to 163.8 ± 21 g; $p < 0.001$). The ELA/FM and TLA/FM required for optimal TSS accumulation were 0.75 m^2 kg-1 and 2.0 m^2 kg-1, respectively, across all sites. A source–sink ratio above these values resulted in high average cane mass and average old cane mass (an indication of excess vigour), while lower values indicated reduced vigour and slowed TSS accumulation. This research provides useful optimal ranges to compare and interpret vine balance metrics measured at those sites.

KEYWORDS: Balance, cane pruning, carbohydrate, crop load, grapevine, growth, pH, Ravaz, ripening, Sauvignon blanc, source–sink, TA, TSS.

INTRODUCTION

Inter-annual yield variations are common in grape production. Between 2017 and 2021, New Zealand Sauvignon blanc yield fluctuated from a low of 10.5 T/ha to a high of 12.9 T/ha with an average of 12.2 T/ha (New Zealand Wine, 2021). An interplay of factors such as the grapevine genotype, environmental conditions, vineyard locations and management practices influence production and composition in any given year (Boursiquot *et al*., 1995; Buttrose, 1970; Coombe and Dry, 2001; Keller, 2015; Parker *et al*., 2011). At the national scale, however, inter-seasonal yield variations are predominantly driven by climate, with temperature around inflorescence initiation, flowering and fruit set playing a key role (Trought, 2005; Vasconcelos *et al*., 2009; Zhu *et al*., 2020). In cooler climates where achieving the ideal ripeness can be challenging, a wide range of management practices that contribute to optimum grape ripeness are implemented, and among these, adequate pruning through node number adjustment is the initial and most cost-effective step (Berkey *et al*., 2011; Greven *et al*., 2014; Greven *et al*., 2015; Keller and Mills, 2007).

Increasing the vine node load generally results in higher yields and delayed ripening in the first year (Greven *et al*., 2014; Jackson *et al*., 1984; Trought *et al*., 2011). However, the trend may not be sustainable over several seasons if the node load exceeds the site and vine capacity, as the vines self-adjust to their new node number by developing fewer shoots and producing smaller and lighter grape bunches (Bravdo *et al*., 1984, Bravdo *et al*., 1985; Greven *et al*., 2014; Jackson *et al*., 1984; Reynolds, 1989; Trought *et al*., 2011). For example, Greven *et al*. (2014) demonstrated that increasing vine node loads from 24 to 72 resulted in a linear yield increase only in the first year, but over subsequent years, high-node vines exhibited reduced bunch number per shoot and average bunch mass compared to low-node vines, leading to all node treatments reaching comparable yields in the fourth year. The same authors (Greven *et al*., 2015) also observed that the period of grape ripening measured by TSS accumulation was 41 days longer on 72-node vines compared with 24-node vines in the first year. In the following seasons, the gap gradually narrowed to five days in the fourth year (Greven *et al*., 2015).

Low temperature and solar radiation may delay the ripening period (Aljibury, 1975; Smart, 1973; Smart and Coombe, 1983). However, maturity delays are also driven by the smaller size of the source (photosynthetically active leaves) relative to the larger size of the sink (Bravdo *et al*., 1985; Keller, 2015; Parker *et al*., 2015; Parker *et al*., 2016; Poni *et al*., 2006; Poni *et al*., 2009; Santesteban and Royo, 2006). A reduction of the source size (or source restriction) through shoot trimming and leaf removal delays TSS accumulation but has no effect on pH and TA, reflecting the dependence of sugar accumulation on photosynthesis rate, whereas pH and TA are not (Parker *et al*., 2015; Parker *et al*., 2016). A dense canopy, however, may increase shading, resulting in high TA concentrations (Keller and Koblet, 1995; Keller *et al*., 1998). On the contrary, increasing the source–sink by fruit thinning (or sink restriction) produces the opposite effect, which is accelerated TSS accumulation with no effect on TA and pH (Dokoozlian and Hirschfelt, 1995; Parker *et al*., 2015; Parker *et al*., 2016). Earlier research on New Zealand Sauvignon blanc (Greven *et al*., 2014; Greven *et al*., 2015; Trought *et al*., 2011; Parker *et al*., 2015; Parker *et al*., 2016) addressed the dynamics of fruit composition relative to the leaf and fruit removal (Parker *et al*., 2015; Parker *et al*., 2016), the effects of increasing retained node numbers on TSS accumulation over four seasons (Greven *et al*., 2014; Greven *et al*., 2015) and on TSS, TA and pH over three seasons (Trought *et al*., 2011). These studies did not investigate the optimal source–sink ratio (TLA/FM, ELA/FM) nor the fruit mass to pruning mass ratio required for adequate fruit ripening.

A source–sink ratio (leaf area to fruit mass) of 0.8–1.2 m^2 kg^{-1}, which corresponds to a fruit mass to cane mass ratio (Ravaz index) of 5–10 kg kg^{-1}, is reported to be the optimum required for berry ripening or TSS accumulation (Kliewer and Dokoozlian, 2005; Kliewer and Weaver, 1971). These ratios were established on grapevine cultivars other than Sauvignon blanc and in growing conditions and viticultural contexts different from New Zealand's, thus warranting an investigation into finding them. Linking berry maturation (TSS, TA, pH) to the source–sink ratio (TLA/FM, ELA/FM), Ravaz index (FM/CM, FM/PM) and retained node numbers is crucial in understanding the drivers of berry ripening and provide context-specific optimal source–sink ratios and Ravaz indices for individual winegrape cultivars.

The objective of the present study was to examine the effects of retained node numbers of Sauvignon blanc on (i) berry maturity and growth as measured by TA, pH, TSS and berry mass from veraison to harvest; (ii) yield and yield components; and (iii) vine balance as measured by TLA/FM, ELA/FM, FM/CM and FM/PM ratios. The study was conducted over two growing seasons in two vineyard sites in Marlborough and another in North Canterbury, New Zealand.

MATERIALS AND METHODS

1. Sites description

The research was conducted in two commercial vineyard blocks, one in the Awatere Valley, Marlborough, New Zealand (GPS: 41°39'43.3"S, 173°59'59.9"E; masl: 140 m) and the other in Waipara, North Canterbury, New Zealand (GPS: 43°06'17.4"S 172°42'26.1"E; masl: <100 m). Two trials were set up in the Awatere Valley vineyard block, which were referred to as Site 1 and Site 2, and the trial in the Waipara vineyard block was referred to as Site 3. A detailed description of both vineyard blocks, including trellis systems, grapevine genotypes, vineyard management and prevailing weather conditions during the experiment, are presented in Epee *et al*. (2022a) and Epee *et al*. (2022b).

In summary, the Awatere Valley vineyard block was established in 2008 and planted with *Vitis vinifera* cv. Sauvignon blanc clone BDX316 grafted on rootstock 101-14 Mgt with rows oriented north-south 2.4 m apart with 1.8 m in-row vine spacing. Vines were trained to a vertical shoot positioned (VSP) system with three canes carrying, on average, 36 nodes (12 nodes per cane) and two spurs of two nodes each. The bottom and top fruiting wires were respectively 1000 mm and 1250 mm from the soil surface on the same vertical plane, and the canopy was restrained to approximately 300 mm wide using movable foliage wires. The canopy was trimmed to a height of 2200 mm three times during the growing season from December to February. Pest and disease management and fertilisation were in line with the organic production standards of the certifying organisation. The vines were drip irrigated when appropriate during the season (except at dormancy) based on soil moisture monitoring from soil moisture sensors. The inter-row was mown and the under-vine mechanically weeded. The yearly average temperature, GDDs (Growing Degree Days base 10 °C temperature) and total annual rainfall were, respectively, 13.2 °C, 1212.4 °C and 211.4 mm in 2019 and 12.9 °C, 1220.8 °C and 558.8 mm in 2020 (Harvest Electronics Ltd, 2021).

The Waipara vineyard block was established in 2006, planted with *Vitis vinifera* cv Sauvignon blanc clone BDX317 grafted on rootstock Schwarzmann. Vines were trained to a vertical shoot positioned (VSP) system with four canes carrying, on average, 48 count nodes on canes (on average, 12 nodes per cane) and two node spurs on either side of the vine trunk. Rows were oriented north-south 2.4 m apart with in-row vine spacing of 2.0 m. Fruiting wires were 900 and 1250 mm from the soil surface and the canopy was restrained to approximately 300 mm wide using movable foliage wires. The canopy was trimmed to a height of 2200 mm three times during the growing season from December to February. The vines were managed according to Sustainable Winegrowing Standards (New Zealand Wine, 2020) and drip irrigated when appropriate (except at dormancy) based on soil moisture monitoring from soil moisture sensors. Yearly average temperature, GDDs and total annual rainfall in 2020 were, respectively, 12.4 °C, 1265.2 °C and 527.6 mm (Harvest Electronics Ltd, 2021).

2. Experimental design and measurements

2.1. Awatere Valley: Site 1 and Site 2

A full description of the experimental design appears in Epee *et al*. (2022a) and Epee *et al*. (2022b). In summary, vines were pruned in winter 2019 according to a 5 (cane node load) × 3 (spur node number) factorial design, and each set of treatments was replicated 15 times to give a total of 75 experimental units (vines) at Site 1. Total node number was also considered as an overall factor, with the total number of nodes on spurs and canes equating to 15 treatments, for a total vine node number ranging from 12 nodes to 56 nodes at Site 1, and from 14 to 56 nodes at Site 2 and Site 3 (Table S1).

On 11 November 2019, about two weeks following the start of budburst at growth stage EL 9, two to three leaves separated (Modified Eichhorn and Lorenz grapevine growth stages (Coombe, 1995)), vines were shoot-thinned to their respective cane and spur node numbers by keeping one shoot per count node and removing shoots growing on all non-count nodes (i.e., shoots on vine head, trunk, basal shoots and excess shoots on count nodes). Cane node number was considered a surrogate for total vine node number due to the non-significance of the interaction of cane node load × spur node number, and due to three-node spurs having a blind node appearing at node position one (Epee *et al*., 2022b). At harvest (on 20 March 2020), 30 berries per vine were randomly sampled on both sides of the canopy, crushed and the juice analysed for TSS with a portable digital refractometer (Atago Co Ltd, USA). Grape bunches of individual vines were hand-harvested, counted and weighed.

In the following growing season (2020/2021), the same node treatments were applied to the same vines as the previous winter, and shoot thinning was conducted as the previous spring. Contrary to the previous season where TSS was only measured at harvest, in the second season, 30 berries were randomly sampled fortnightly on each vine from EL 33 (berries still hard and green) to EL 38 (berries harvest-ripe) on four dates from 9 February to 22 March 2021. At each sampling time, berries were stored in a cooler bag and taken to the laboratory for analysis within 48 hours. Each sample was weighed, crushed and sieved, and the juice was extracted for analysis. TSS was measured as indicated above in 2019/2020. Titratable acidity was measured using the endpoint titration (tartaric acid equivalents in g/L) using 0.1 mol NaOH to pH 8.4 with an auto-titrator (Metrohm USA), and pH was measured using the same auto-titrator (Metrohm, USA) pH meter. On 22 March 2021, grape bunches were hand-harvested separately from canes, spurs and the vine head, then counted and weighed.

Vine total leaf area (TLA) and exposed leaf area (ELA) were calculated on 22 February, four weeks before harvest. TLA was estimated by randomly sampling one healthy shoot located at the proximal section to the trunk of the bottom cane, measuring the midrib length of all leaves on the shoot (including all leaves on lateral shoots when present) and then multiplying the total shoot leaf area by the total number of shoots on the vine (Dokoozlian and Kliewer, 1995). In total, 10 leaves from each of the 10 vines were randomly collected at the 2020 harvest. The lamina of each leaf was then scanned using the Epson XP-3100 Series digital scanner, and the area was computed using scanned images and the R package LeafArea (Katabuchi, 2015). The mid-rib of each leaf was measured and used to develop a regression function ($y = 41.8 - 22.7x + 4.9x^2 - 0.16x^3$; $R^2 = 0.96$, $p < 0.001$) relating midrib leaf length to leaf area. The same regression function was used the following season.

To estimate ELA, digital photos (with scales embedded) of one side of the grapevine's canopies were taken with a Nikon D5500 DSLR Camera (Nikon, Japan) on a white

TABLE 1. Total soluble solids (TSS) measured at harvest in 2019/2020 and 2020/2021 growing seasons.

Cane node loads	Site 1 season 2019/2020 (measured on 20.03.2020)	Site 1 season 2020/2021 (measured on 22.03.2021)	*p-value**	Site 2 season 2020/2021 (measured on 22.03.2021)	Site 3 season 2020/2021 (measured on 15.03.2021)
	Total soluble solids—TSS (°Brix)				
N10	18.8 ± 0.3 a|B	21.7 ± 0.2 a|A	< 0.001	22.3 ± 0.2 a	19.7 ± 0.2 a
N20	18.3 ± 0.3 ab|B	21.6 ± 0.2 a|A	< 0.001	22.2 ± 0.1 ab	19.7 ± 0.2 a
N30	17.9 ± 0.3 ab|B	21.5 ± 0.3 a|A	< 0.001	21.7 ± 0.2 ab	19.4 ± 0.1 ab
N40	17.4 ± 0.3 b|B	21.3 ± 0.2 a|A	< 0.001	21.4 ± 0.3 ab	18.8 ± 0.2 b
N50	16.2 ± 0.3 c|B	20.9 ± 0.3 a|A	< 0.001	21.1 ± 0.3 c	18.8 ± 0.2 b
p-value	< 0.001	ns		< 0.05	< 0.01

N10, N20, N30, N40 and N50 refer to total node numbers on vine's canes equalling 10, 20, 30, 40 and 50 nodes, respectively. Values are mean ± standard error of the mean of 15 vines at Site 1 and 10 vines at Sites 2 and 3. Means sharing the same lowercase letter in a column (cane node load comparison) or the same uppercase letter in a row (seasons comparison at Site 1) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$). * *p-value* indicates the level of significance of the variable measured at Site 1 between the first and second season.

TABLE 2. Berry total soluble solids (TSS) accumulation rate modelled with the exponential three parameters growth curve across three sites in the 2020/2021 growing season.

Sites	Cane node load	Day 8 °Brix	Day 21 °Brix	Duration 8 to 21 °Brix (Days)
Site 1	N10	13 Feb. a	18 Mar. b	34.2 ± 0.6 b
	N20	14 Feb. a	20 Mar. b	33.5 ± 0.6 b
	N30	14 Feb. a	18 Mar. b	33.2 ± 0.7 b
	N40	13 Feb. a	22 Mar. a	36.7 ± 0.9 a
	N50	13 Feb. a	22 Mar. a	36.5 ± 0.8 a
	p-value	ns	< 0.05	< 0.01
Site 2	N10	14 Feb. a	18 Mar. c	31.4 ± 0.5 c
	N20	13 Feb. a	18 Mar. c	33.6 ± 0.7 bc
	N30	13 Feb. a	19 Mar. abc	35.5 ± 1.4 abc
	N40	13 Feb. a	22 Mar. ab	37.6 ± 2.1 ab
	N50	13 Feb.a	23 Mar. a	38.2 ± 2.0 a
	p-value	ns	< 0.05	< 0.05
Site 3	N10	18 Feb. a	1 Apr. b	39.5 ± 2.9 b
	N20	18 Feb. a	30 Mar. b	39.5 ± 1.0 b
	N30	18 Feb. a	30 Mar. b	40.2 ± 0.5 b
	N40	19 Feb. a	3 Apr. ab	42.7 ± 1.3 ab
	N50	19 Feb. a	5 Apr. a	45.5 ± 2.3 a
	p-value	ns	0.05	0.05

Means followed by the same letter within a column are not significantly different with the protected least significant difference test at $p \leq 0.05$.

background. Photos were transferred into the ImageJ software (The National Institutes of Health, USA) from which the green canopy area was segmented and calculated. The vine's total ELA was calculated as twice the one-side area as determined by the software, and the same procedure was followed for both seasons.

In winter, vines were pruned, and for each vine, the wood was sorted into cane (the dormant shoot or one-year-old wood) and old cane (or two-year-old wood) and then weighed separately. The average cane mass was calculated by dividing the mass of all canes by the total number of canes pruned off, and the average old cane mass was obtained by dividing the mass of old canes by the number of old canes pruned off. The total cane mass was then adjusted by adding the estimated mass of retained canes left on the vine at pruning from the average cane mass.

In winter 2020, 50 vines were selected within the same vine row and pruned for a 5 cane node load × 2 spur node number factorial designed experiment (referred to as Site 2) with five replicates and with the same five node loads as Site 1 vines, in combination with two node numbers on spurs (two and three node spurs). The same measurements were collected at Site 1 in 2020/2021. Site 2 represented a seasonal repeat of the 2019/2020 experiment at Site 1, which excluded the carry-over effect of the previous year's pruning treatments.

2.2. Waipara: Site 3

At Site 3, 50 vines along a south/north-oriented row were pruned in winter 2020 with the same node treatments as at Site 2. Measurements were the same as at Site 2 except that berry sampling for TSS, TA, pH and berry mass was done from 2 February to 15 March 2021 (harvest day) and TLA and ELA were measured on 15 February 2021 (four weeks before harvest).

2.3. Curve fitting and statistical analyses

A 3-parameter rise to maximum exponential model (Fekedulegn *et al*., 1999) was fitted to TSS data, from which the time from 8 to 21 °Brix was interpolated.

$$Y = A + Be^{(CX)} \quad (1)$$

where A is the Y asymptote, B is the displacement along the x-axis, C is the rate of increase, X is the time interval (in days) and e is Euler's Number.

The optimal source–sink ratio was determined by plotting ELA/FM and TLA/FM (x-coordinate) with TSS (y-coordinate), then fitting the best curve (least sum of square error) to the data points. The optimum point on the curve was set at 90 % of the Y asymptote value and its projection on the x-coordinate gave the optimal source–sink value.

All dependent variables (TSS, TA, pH, berry mass, yield, yield components, cane mass, old cane mass, average cane mass, average old cane mass and vine balance ratios) were compared with the Analysis of Variance (ANOVA) and Fisher's Least Significant Difference Test (LSD). The independent variables were the factors: cane node load and spur node number. Before running ANOVA, Levene's test was conducted to check the homogeneity of variances, and the Shapiro–Wilk test was applied to check whether data were normally distributed. The two ANOVA assumptions were met. Considering that there was no interaction between cane node load and spur node number and that spur node number had no significant effect on all dependent variables, only the effect of the factor cane node load was presented and used as a surrogate for the total vine's node number. The significance level for all tests was set at $p < 0.05$. Data were analysed in RStudio Version 4.0.5 (R Core Team, 2021). The following R packages were used: dplyr (Wickham *et al*., 2021), ggpubr (Kassambara, 2020), agricolae (Mendiburu, 2020), Rmisc (Hope, 2013) and Car (Fox and Weisberg, 2019).

RESULTS

1. TSS, TA and pH response to node load

Total Soluble Solids (TSS) concentration at harvest was greater with decreasing node numbers at Site 1 in 2019/2020 and at Site 2 and Site 3 in 2020/2021 (Table 1). At Site 1 in the 2019/2020 harvest, grapes on 10-node vines had significantly higher concentrations of TSS (18.8 ± 0.3 °Brix) than on 50-node vines (16.2 ± 0.3 °Brix, $p < 0.001$; Table 1). Although the differences were not significant in the 2020/2021 harvest, there was still a clear trend similar to that of the previous harvest. In 2019/2020, none of the five node treatments reached the maturity of 20 °Brix. The following season, harvest was on almost the same day of the year as the previous season and yet all the vine node loads recorded 20 °Brix or more (Table 1).

At Sites 2 and 3 (Table 1) low-node vines had significantly higher TSS concentrations at harvest (22.3 and 19.7 °Brix, respectively) than 50-node vines (21.1 and 18.8 °Brix, respectively, $p < 0.05$). Overall, the time from 8 to 21 °Brix was significantly longer on 50-node vines compared with 10-node vines (respectively 31.4 and 38.2 days at Site 2, $p < 0.01$) (Table 2). In 2020/2021, high-node vines accumulated TSS at a slower rate than low-node vines, resulting in an extension of the ripening period from veraison to harvest (from 34.2 ± 0.6 days on 10-node vines to 36.5 ± 0.8 on 50-node vines) (Table 2).

Berry juice pH and TA at Sites 2 and 3 were generally unaffected by node treatments from Day 1 to Day 28, except on Day 1 at Site 2, where N10 vines had the lowest pH (Figure 1). At Site 1, however, node treatments had significant effects on TA at every time point but almost no effect on pH—with the exception of Day 28, when N10 vines had significantly lower pH (Figure 1).

2. Yield and yield components

2.1. Seasonal variations of yield and yield components over two years at Site 1

In general, bunch mass per vine (vine yield) increased with increasing node numbers whereas a drop in vine yield was observed in the second season of node treatments (Figure 2a).

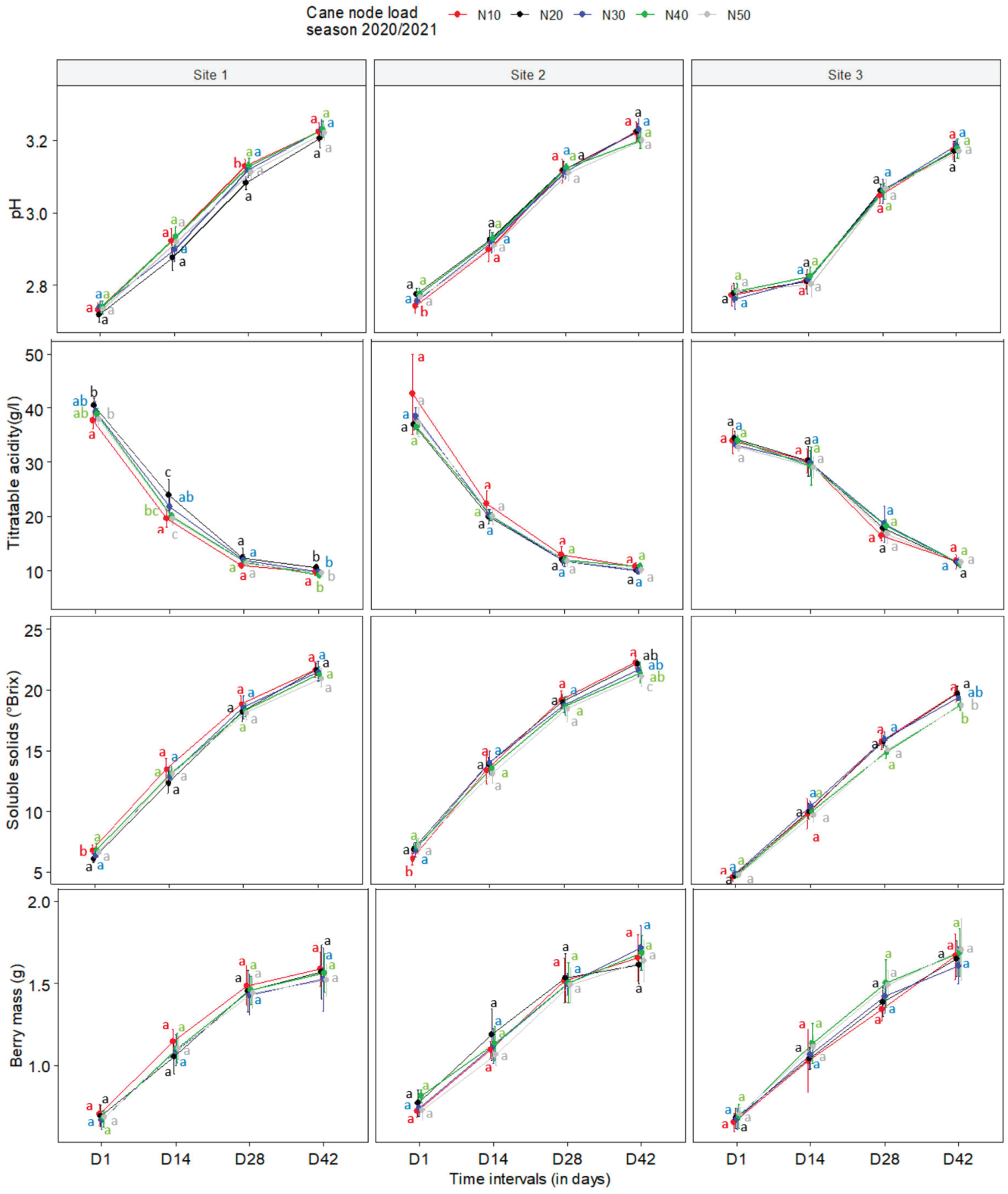


FIGURE 1. Berry composition and mass on four dates at fortnightly intervals on 9 February (D1), 23 February (D14), 8 March (D28) and 22 March 2021 (D42) at Site 1 and 2, and on 2 February (D1), 16 February (D14), 1 March (D18) and 15 March 2021 (D42) at Site 3. N10, N20, N30, N40 and N50 refer to the total node number on vine's canes being equal to 10, 20, 30, 40 and 50 nodes, respectively. Points represent mean ± standard error of the mean with n = 15 vines for Site 1 and 10 vines for Site 2 and 3 for each cane node treatment. Means sharing the same letter on a given date are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

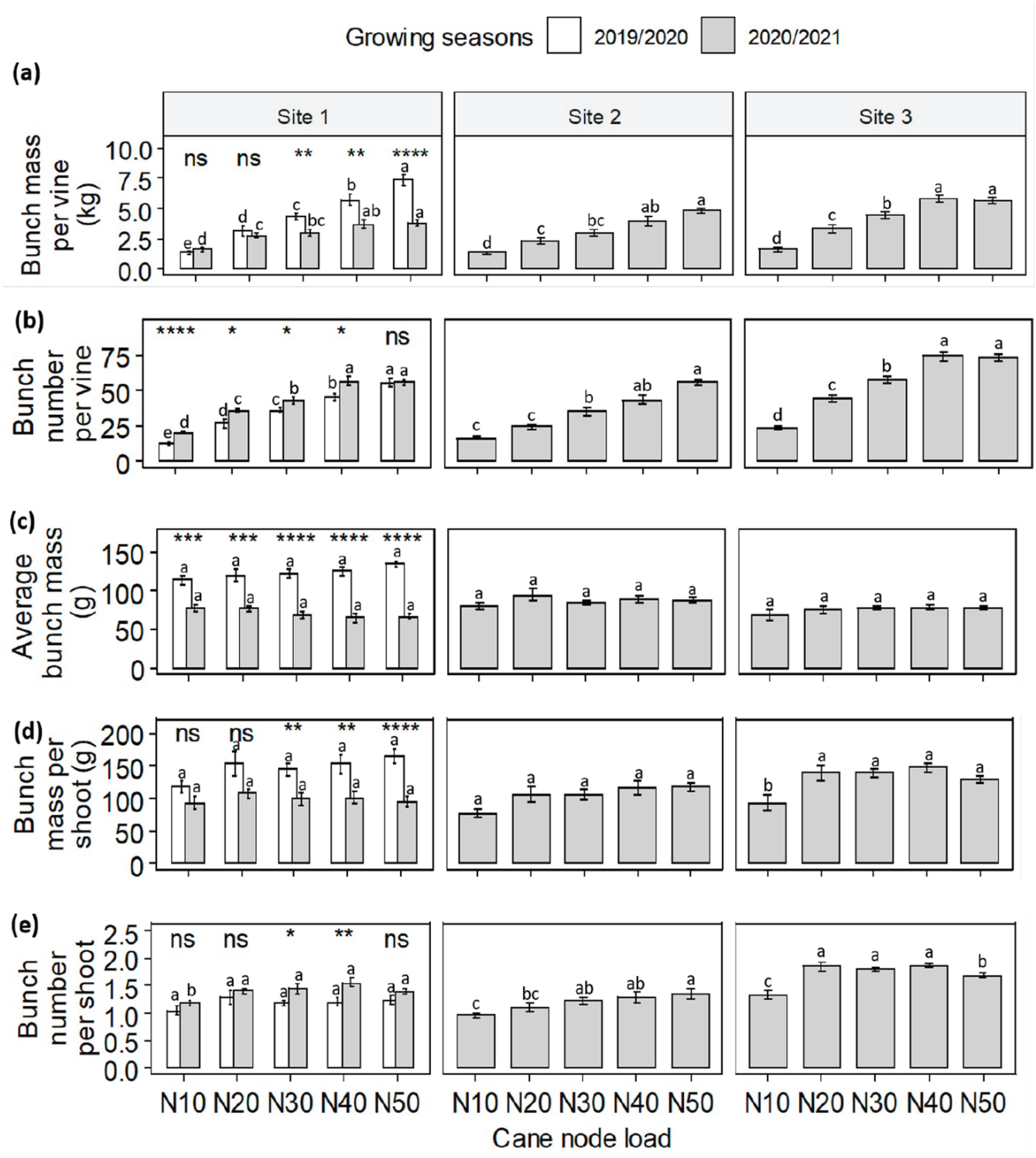


FIGURE 2. Effect of node load on yield components. N10, N20, N30, N40 and N50 refer to total node numbers on vine's canes equalling 10, 20, 30, 40 and 50 nodes, respectively. Points and bars represent the mean ± standard error of the mean of 15 vines for Site 1 and 10 vines for Site 2 and Site 3. Means sharing the same letter across different node treatments (node load comparison) are not significantly different with the Fisher's protected LSD test, $p \leq 0.05$. For each individual node treatment at Site 1, the significance of the difference between both seasons is indicated by the significance symbols of ANOVA: 'ns' not significant and $p > 0.05$; '*', $p < 0.05$; '**' $p < 0.01$; '***', $p < 0.001$; '****', $p < 0.0001$.

At Site 1 and in both seasons, the total bunch mass per vine and bunch number per vine increased with increasing node loads (Figure 2a,b). Between 2019/2020 and 2020/2021, the total bunch mass, average bunch mass per vine and bunch mass per shoot dropped respectively by 28, 43 and 33 % on average across all node treatments (Figure 2a,c,d). On all node loads at Site 1, the bunch number per vine rose substantially by 21 % on average across all node loads in 2020/2021, with 10-node vines recording the highest rise (63 %; $p < 0.0001$) and 50-node vines the lowest (1 %; $p < 0.05$; Figure 2b). Similarly, the bunch number per shoot increased in 2020/2021 by 17 % on average across all node treatments. The increase was significant on 30-node (22 %; $p < 0.05$) and 40-node vines (29 %; $p < 0.01$) but not statistically significant on other node treatments (Figure 2e). When the four yield components were considered together it appeared that the drop in vine yield between 2019/2020 and 2020/2021 at Site 1 was mainly driven by the diminution of the average bunch mass per vine and bunch mass per shoot (Figure 2c). The relative rise in bunch number per vine and bunch number per shoot was not sufficient to offset the depressing effect of low bunch mass. Overall, yield components were affected by both inter-seasonal weather variations (Figure S1) and node load treatments at Site 1, except for berry mass which remained stable during ripening (Figure 1).

2.2. Yield and yield components in the 2020/2021 season across all sites

2.2.1. Whole vin

The total bunch mass per vine increased linearly with increasing node loads across all three sites ($R^2 = 0.9$, $p < 0.001$ for Site 1 and 2, $R^2 = 0.9$, $p < 0.05$ for Site 3; Figure 2a, Figure S2). The bunch number per vine equally followed a similar pattern of a linear increase at all three sites ($R^2 = 0.9$, $p < 0.001$ for Site 1 and 2, $R^2 = 0.9$, $p < 0.01$ for Site 3; Figure S3). Bunch mass per shoot was stable across node treatments at Site 2 and over both seasons at Site 1 (Figure 2d). At all sites a clear trend for 10-node vines having the lowest bunch mass per shoot was visible and this trend was significant at Site 3 ($p < 0.001$, Figure 2d). Berry mass did not change significantly across all node treatments at each site in the 2020/2021 growing season (Figure 1).

2.2.2. Vine parts

The canes contributed the greatest mass to the vine yield with smaller numbers and mass borne on spurs and non-count headshoots (Table 3). The fewer shoots that developed on the vine head bore fewer and lighter grape bunches (Tables 4 and 5). At Site 1, all yield components on cane (except for total bunch mass and shoot number) were significantly higher on N10 and N20 vines (Table 3–5). At Site 2, no significant differences were noted across node treatments on cane yield components, except for shoot

TABLE 3. Bunch mass and bunch number on cane, spur and vine head at Site 1 and Site 2 in the 2020/2021 growing season.

Sites	Cane node loads	Bunch mass on each vine part (kg)			*p-value*	Bunch number on each vine part			*p-value*
		Cane*	Spur#	Head		Cane*	Spur#	Head	
Site 1	N10	1.24 ± 0.0 a|A	0.18 ± 0.0 a|B	0.11 ± 0.1 a|B	< 0.001	15.0 ± 0.6 a|A	2.8 ± 0.3 a|B	2.3 ± 0.5 a|B	< 0.001
	N20	1.17 ± 0.0 a|A	0.19 ± 0.0 a|B	0.10 ± 0.0 a|B	< 0.001	15.1 ± 0.4 a|A	2.5 ± 0.3 a|B	2.3 ± 1.3 a|B	< 0.001
	N30	0.87 ± 0.1 b|A	0.19 ± 0.0 a|B	0.00 ± 0.0 a|B	< 0.001	12.4 ± 0.7 b|A	2.6 ± 0.3 a|B	2.0 ± 0.5 a|B	< 0.001
	N40	0.85 ± 0.0 b|A	0.13 ± 0.0 a|B	0.05 ± 0.0 a|B	< 0.001	12.9 ± 0.6 b|A	2.1 ± 0.3 a|B	1.3 ± 0.2 a|B	< 0.001
	N50	0.88 ± 0.0 b|A	0.12 ± 0.0 a|B	0.08 ± 0.0 a|B	< 0.001	12.8 ± 0.4 b|A	2.0 ± 0.2 a|B	1.8 ± 0.4 a|A	< 0.001
p-value		< 0.001	ns	ns		< 0.001	ns	ns	
Site 2	N10	1.09 ± 0.0 a|A	0.11 ± 0.0 a|B	0.09 ± 0.0 a|B	< 0.001	12.7 ± 1.0 a|A	2.0 ± 0.3 a|B	2.0 ± 1.0 a|B	< 0.001
	N20	0.97 ± 0.1 a|A	0.1.6 ± 0.0 a|B	0.06 ± 0.0 a|B	< 0.001	10.0 ± 0.9 b|A	2.0 ± 0.1 a|B	1.5 ± 0.5 a|B	< 0.001
	N30	0.85 ± 0.0 a|A	0.21 ± 0.0 a|B	0.03 ± 0.0 a|B	< 0.001	9.9 ± 0.9 b|A	2.5 ± 0.4 a|B	1.0 ± 0.0 a|B	< 0.001
	N40	0.90 ± 0.0 a|A	0.16 ± 0.0 a|B	0.06 ± 0.0 a|B	< 0.001	9.7 ± 0.6 b|A	2.2 ± 0.3 a|B	1.6 ± 0.6 a|B	< 0.001
	N50	1.16 ± 0.0 a|A	0.12 ± 0.0 a|B	0.04 ± 0.0 a|B	< 0.001	13.1 ± 0.5 a|A	1.6 ± 0.2 a|B	1.5 ± 0.5 a|B	< 0.001
p-value		ns	ns	ns		< 0.05	ns	ns	

N10, N20, N30, N40 and N50 refer to the total node number on vine's canes equals 10, 20, 30, 40 and 50 nodes, respectively. Values are mean ± standard error of 15 vines for Site 1 and 10 vines for Site 2. Means sharing the same lowercase letter in a column (cane node loads comparison) or the same uppercase letter in a row (comparison between vine organs) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$). * For cane, values of total bunch mass and bunch number were normalised by dividing the sum from all vine canes by its total cane number (i.e., by one for N10 vines, two for N20 vines, three for N30 vines and four for N40 and N50 vines). # For spur, values are normalised by dividing the bunch mass from all vine's spur by its total spur number (i.e., by two for all cane node load).

TABLE 4. Average bunch mass per vine and average bunch mass per shoot from three grapevine parts (cane, spur and vine head) at Site 1 and Site 2 in the 2020/2021 growing season.

Sites	Cane node loads	Average bunch mass (g)			*p-value*	Bunch mass per shoot (g)			*p-value*
		Cane	Spur	Head		Cane	Spur	Head	
Site 1	N10	82.0 ± 6 a|A	70.6 ± 6 a|B	40.9 ± 5 a|C	< 0.01	153.5 ± 15 a|A	79.7 ± 14 a|B	5.8 ± 2 a|C	< 0.001
	N20	77.6 ± 4 a|A	75.0 ± 5 a|A	56.7 ± 7 a|B	< 0.05	138.9 ± 7 ab|A	84.5 ± 10 a|B	5.5 ± 3 a|C	< 0.001
	N30	68.5 ± 4 b|A	67.8 ± 7 a|A	40.2 ± 8 a|B	< 0.05	111.5 ± 10 bc|A	82.5 ± 13 a|A	9.0 ± 3 a|B	< 0.001
	N40	66.4 ± 5 b|A	65.9 ± 8 a|A	39.4 ± 9 a|B	< 0.05	111.0 ± 11 bc|A	72.1 ± 9 a|B	10.3 ± 6 a|C	< 0.001
	N50	67.7 ± 3 b|A	59.5 ± 6 a|B	45.2 ± 12 a|C	< 0.05	106.7 ± 9 c|A	74.6 ± 13 a|B	9.5 ± 4 a|C	< 0.001
p-value		< 0.01	ns	ns		< 0.05	ns	ns	
Site 2	N10	95.1 ± 8 a|A	53.6 ± 8 a|AB	61.8 ± 18 a|B	< 0.01	139.5 ± 9 a|A	50.2 ± 17 a|B	4.0 ± 2 a|C	< 0.001
	N20	87.2 ± 2 a|A	80.4 ± 8 a|AB	50.3 ± 31 a|B	< 0.05	122.4 ± 11 a|A	87.5 ± 11 a|A	1.3 ± 1 a|B	< 0.001
	N30	86.0 ± 3 a|A	81.6 ± 6 a|A	34.0 ± 21 a|B	< 0.01	118.6 ± 9 a|A	123.6 ± 21 a|A	1.8 ± 1 a|B	< 0.001
	N40	92.3 ± 5 a|A	74.5 ± 10 a|A	30.6 ± 11 a|B	< 0.01	133.6 ± 12 a|A	108.0 ± 30 a|A	7.7 ± 6 a|B	< 0.001
	N50	88.9 ± 4 a|A	69.5 ± 6 a|B	24.3 ± 20 a|C	< 0.001	128.9 ± 9 a|A	88.2 ± 14 a|B	3.7 ± 3 a|C	< 0.001
p-value		ns	ns	ns		ns	ns	ns	

N10, N20, N30, N40 and N50 refer to the total node number on vine's canes equals 10, 20, 30, 40 and 50 nodes, respectively. Values are mean ± standard error of 15 vines for Site 1 and 10 vines for Sites 2 and 3. Means sharing the same lowercase letter in a column (cane node load comparison) or the same uppercase letter in a row (comparison between vine organs) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

TABLE 5. Shoot number and bunch number per shoot from three grapevine parts (canes, spurs and vine head) at Site 1 and Site 2 in the 2020/2021 growing season.

Sites	Cane node loads	Shoot number			*p-value*	Bunch number per shoot			*p-value*
		Cane*	Spur#	Head (H)		Cane	Spur	Head	
Site 1	N10	8.3 ± 0.4 a|A	2.0 ± 0.1 a|B	5.1 ± 0.6 a|B	< 0.001	1.8 ± 0.0 a|A	1.1 ± 0.1 a|B	0.1 ± 0.0 a|C	< 0.001
	N20	8.4 ± 0.2 a|A	2.2 ± 0.1 a|B	4.7 ± 0.6 ab|B	< 0.001	1.8 ± 0.0 ab|A	1.1 ± 0.0 a|B	0.1 ± 0.1 a|C	< 0.001
	N30	7.7 ± 0.1 a|A	2.0 ± 0.1 a|B	3.2 ± 0.4 bc|B	< 0.001	1.6 ± 0.0 bc|A	1.2 ± 0.1 a|B	0.3 ± 0.1 a|C	< 0.001
	N40	7.7 ± 0.1 a|A	1.8 ± 0.1 a|B	1.8 ± 0.3 bc|B	< 0.001	1.7 ± 0.0 bc|A	1.2 ± 0.1 a|B	0.6 ± 0.1 a|C	< 0.001
	N50	8.3 ± 0.3 a|A	1.6 ± 0.1 a|B	3.2 ± 0.5 bc|B	< 0.001	1.6 ± 0.0 c|A	1.2 ± 0.1 a|B	0.2 ± 0.1 a|C	< 0.001
p-value		ns	ns	< 0.001		< 0.05	ns	ns	
Site 2	N10	7.9 ± 0.3 b|A	2.0 ± 0.1 a|B	5.7 ± 0.6 a|B	< 0.001	1.6 ± 0.12 a|A	0.9 ± 0.18 a|B	0.1 ± 0.0 a|C	< 0.00
	N20	8.0 ± 0.2 ab|A	1.9 ± 0.1 a|B	3.7 ± 0.4 b|B	< 0.001	1.3 ± 0.12 a|A	1.2 ± 0.19 a|A	0.1 ± 0.0 a|B	< 0.001
	N30	7.2 ± 0.5 b|A	1.6 ± 0.1 a|B	3.5 ± 0.6 b|B	< 0.001	1.4 ± 0.07 a|A	1.5 ± 0.21 a|A	0.1 ± 0.0 a|B	< 0.001
	N40	6.9 ± 0.4 b|A	1.5 ± 0.2 a|B	3.7 ± 0.5 b|B	< 0.001	1.5 ± 0.13 a|A	1.4 ± 0.19 a|A	0.2 ± 0.1 a|B	< 0.001
	N50	9.2 ± 1.7 a|A	1.2 ± 0.2 a|B	2.5 ± 0.4 b|B	< 0.001	1.5 ± 0.10 a|A	1.3 ± 0.19 a|A	0.2 ± 0.1 a|B	< 0.001
p-value		< 0.01	ns	< 0.01		ns	ns	ns	

N10, N20, N30, N40 and N50 refer to the total node number on vine's canes, which equals 10, 20, 30, 40 and 50 nodes, respectively. Values are mean ± standard error of 15 vines for Site 1 and 10 vines for Sites 2 and 3. Means sharing the same lowercase letter in a column (cane node load comparison) or the same uppercase letter in a row (comparison between vine organs) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$). * For canes, values of Shoot number are normalised by dividing the sum from all vine canes by the total cane number (i.e., by one for N10 vines, two for N20 vines, three for N30 vines and four for N40 and N50 vines). # For spur, values are normalised by dividing the bunch mass from all vine's spurs by the total vine's spur number (i.e., by two for all cane node load).

TABLE 6. Effect of increasing node load on leaf area.

Cane node loads	Site 1 season 2019/2020	Site 1 season 2020/2021	*p-value**	Site 2 season 2020/2021	Site 3 season 2020/2021
	Total leaf Area—TLA (m^2)				
N10	6.67 ± 0.6 b|A	4.67 ± 0.6 c|A	ns	6.94 ± 1.2 c	8.39 ± 0.5 d
N20	6.21 ± 0.2 b|A	7.50 ± 0.5 b|A	ns	6.88 ± 0.4 c	8.86 ± 1.1 cd
N30	9.05 ± 0.6 a|A	7.48 ± 0.7 b|A	ns	8.95 ± 0.8 b	11.91 ± 0.6 bc
N40	8.57 ± 0.6 a|A	8.99 ± 0.9 ab|A	ns	8.85 ± 0.8 b	14.16 ± 1.7 ab
N50	9.22 ± 0.4 a|A	9.52 ± 0.7 a|A	ns	13.2 ± 1.1 a	16.10 ± 1.2 a
p-value	< 0.001	< 0.001		< 0.001	< 0.001
	Exposed Leaf Area—ELA (m^2)				
N10	2.12 ± 0.1 b|B	2.59 ± 0.1 c|A	< 0.05	2.98 ± 0.2 c	3.62 ± 0.1 b
N20	2.25 ± 0.1 b|B	3.10 ± 0.1 b|A	< 0.001	3.07 ± 0.1 c	4.09 ± 0.0 a
N30	2.75 ± 0.1 a|B	3.42 ± 0.1 ab|A	< 0.001	3.27 ± 0.1 bc	4.38 ± 0.1 a
N40	2.89 ± 0.1 a|B	3.49 ± 0.1 ab|A	< 0.001	3.71 ± 0.1 ab	4.27 ± 0.1 a
N50	3.08 ± 0.1 a|B	3.55 ± 0.1 a|A	< 0.05	3.89 ± 0.1 a	4.18 ± 0.1 a
p-value	< 0.001	< 0.001		< 0.01	< 0.01
	Exposed Leaf Area to Fruit Mass ratio—ELA/FM (m^2 kg^{-1})				
N10	1.51 ± 0.2 a|A	1.87 ± 0.2 a|A	ns	2.27 ± 0.2 a	2.67 ± 0.5 a
N20	1.00 ± 0.2 b|A	1.20 ± 0.0 b|A	ns	1.48 ± 0.1 b	1.33 ± 0.1 b
N30	0.67 ± 0.0 bc|B	1.30 ± 0.1 b|A	< 0.001	1.14 ± 0.0 bc	1.00 ± 0.0 b
N40	0.58 ± 0.0 c|C	1.06 ± 0.1 b|A	< 0.001	1.04 ± 0.1 c	0.76 ± 0.0 b
N50	0.45 ± 0.0 c|C	1.01 ± 0.0 b|A	< 0.001	0.81 ± 0.0 c	0.76 ± 0.0 b
p-value	< 0.001	< 0.01		< 0.001	< 0.001
	Total Leaf Area to Fruit Mass ratio—TLA/FM (m^2 kg^{-1})				
N10	4.40 ± 0.3 a|A	3.93 ± 0.8 a|A	ns	5.29 ± 1.1 a	6.53 ± 1.8 a
N20	3.41 ± 1.3 ab|A	2.90 ± 0.2 a|A	ns	3.14 ± 0.5 b	2.73 ± 0.3 b
N30	2.21 ± 0.2 bc|A	2.83 ± 0.4 a|A	ns	3.37 ± 0.4 b	2.80 ± 0.2 b
N40	1.41 ± 0.1 c|B	3.02 ± 0.4 a|A	< 0.01	2.51 ± 0.3 b	2.50 ± 0.3 b
N50	1.38 ± 0.2 c|B	2.94 ± 0.2 a|A	< 0.001	2.63 ± 0.2 b	2.95 ± 0.3 b
p-value	< 0.01	ns		< 0.05	< 0.01

N10, N20, N30, N40 and N50 refer to the total node number on vine's canes equals 10, 20, 30, 40 and 50 nodes, respectively. Values are mean ± standard error of the mean of 15 vines for Site 1 and 10 vines for Sites 2 and 3. Means sharing the same lowercase letter in a column (cane node load comparison) or the same uppercase letter in a row (seasons comparison at Site 1) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$). * *p-value* indicates the level of significance of the variable measured at Site 1 between the first and second season.

number and bunch number, which were significantly higher on N50 vines because they bore more shoots on canes and thus more bunches than N20 to N40 treatments (Table 3–5). When the yield components of the three vine parts were compared (Table 3–5), they were the highest on the cane, high on the spur and the lowest on the vine head.

2.2.3. Whole vine and vine part

Comparing the effect of increased node number on yield components for the whole vine and individual vine parts revealed another aspect of the vine's physiological response. Overall, the spur and head did not respond to node treatments, all node treatments had statistically similar values whereas the cane responded the most (especially at Site 1). After normalising all cane yield components on a per cane basis (see note Tables 3 and 5), almost all of them (except for cane shoot number at Site 2) decreased in value with increasing node number (Table 3–5); the opposite of what was observed on vine yield components which increased in value with increasing node numbers (Figure 2).

3. Vine balance ratios and their components

3.1. Source size (total leaf area—TLA, exposed leaf area–ELA) and source–sink ratios (total leaf area to fruit mass—TLA/FM, exposed leaf area to fruit mass—ELA/FM)

Over both seasons and across all three sites, no clear relationship was found between TLA and ELA (Figure S4). At Site 1, the vine TLA and ELA increased with node load ($p < 0.001$) evidently because of the high number of shoots on high-node vines, given that the shoot leaf area was similar across all node loads (Table 6, Figure S5). Between 2019/2020 and 2020/2021, the vine TLA did not vary significantly, whereas ELA increased significantly across all node treatments ($p < 0.001$; Table 6) possibly due to seasonal variations.

Contrary to TLA and ELA, TLA/FM and ELA/FM at Site 1 decreased with increasing node load ($p < 0.001$); however, with different magnitudes of responses as a function of site and season (Table 6). The high TLA/FM and ELA/FM noted on N10 vines was likely caused by the significantly greater number of head shoots of very low fruitfulness (i.e., carrying smaller and fewer grape bunches) they produced compared with N50 vines ($p < 0.01$; Table 4). From the first trial year in 2019/2020 to the second in 2020/2021, TLA/FM and ELA/FM rose significantly on N40 and N50 vines ($p < 0.001$) but remained stable on low-node vines (Table 6). Since vine TLA was constant over both seasons, the change in TLA/FM was driven by the variation in the total bunch mass per vine (Figure 2a), whereas the change in the ELA/FM was the result of both ELA and the total bunch mass per vine variations.

The patterns described at Site 1 for TLA, ELA, TLA/FM and ELA/FM were very similar at Site 2 and 3, with vine TLA and ELA increasing with node load ($p < 0.001$) whereas TLA/FM and ELA/FM were decreased with node load ($p < 0.01$).

When the total bunch mass per vine (vine yield), TSS concentrations at harvest and the source–sink ratios (ELA/FM and TLA/FM) were considered together, harvest TSS was low on high-yield vines (N40 and N50 vines)

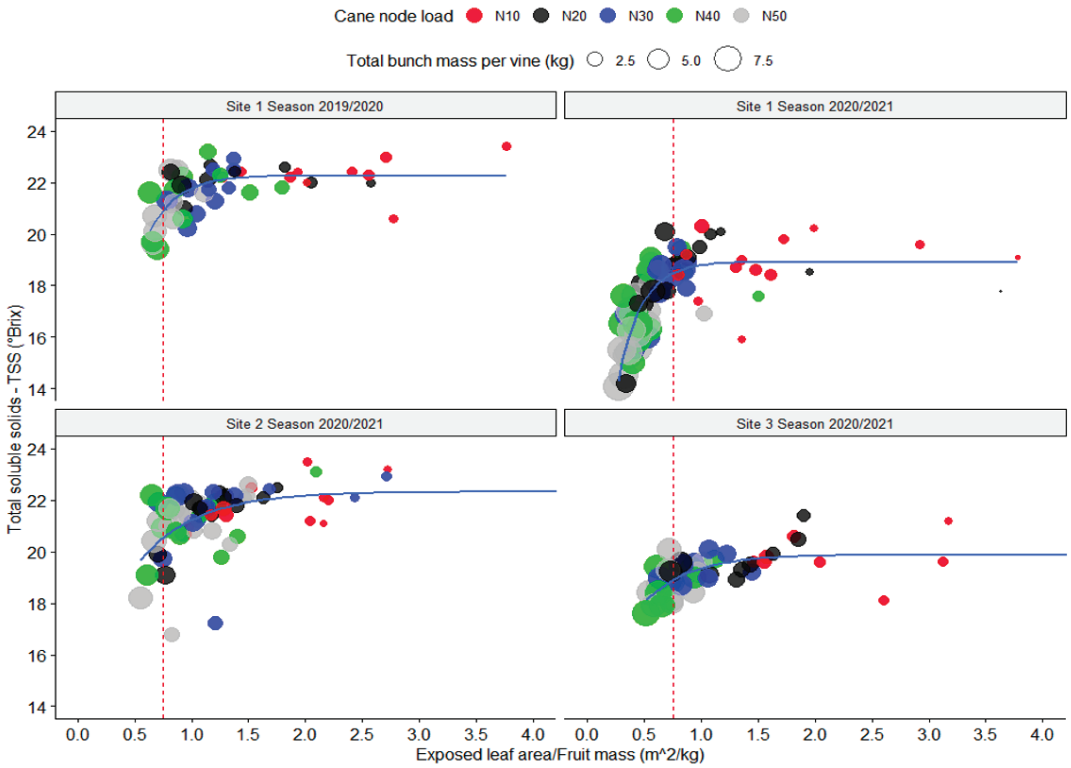


FIGURE 3. Relationship between total soluble solids (TSS), total bunch mass per vine, node load and exposed leaf area to fruit mass ratio (ELA/FM).

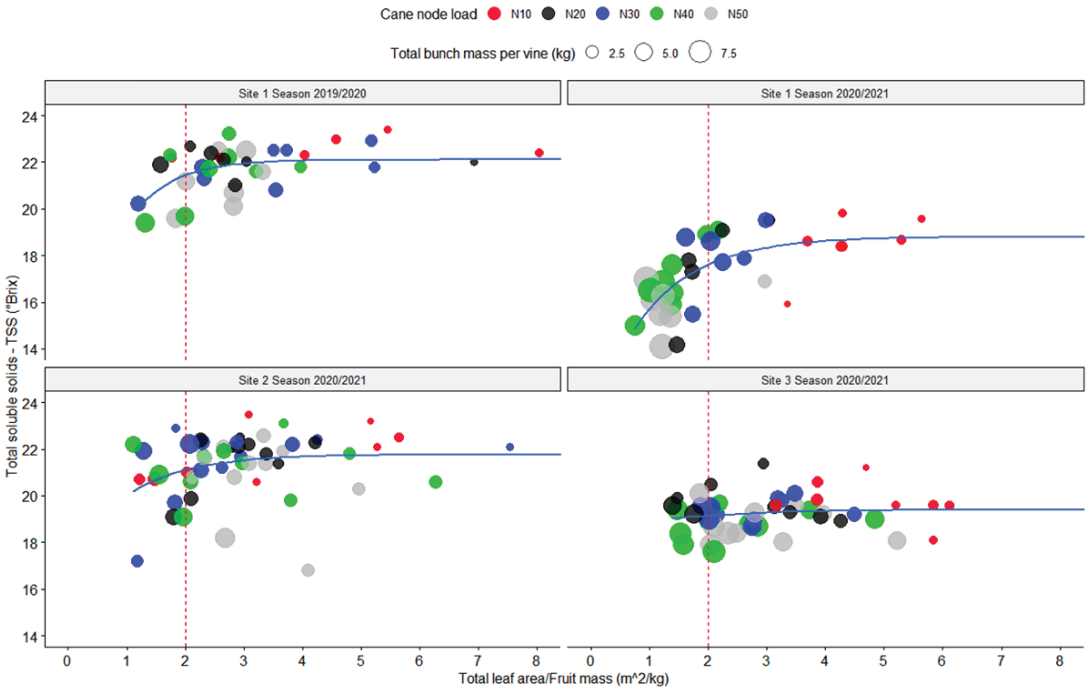


FIGURE 4. Relationship between total soluble solids (TSS), total bunch mass per vine, node load and total leaf area to fruit mass ratio (TLA/FM).

but high on low-yield vines (N10 vines) with N30 vines having intermediate values (Figures 3 and 4). The optimal ELA/FM across all three sites was 0.75 m^2 kg^{-1}, and the optimal TLA/FM at Site 1 and Site 2 was 2.0 m^2 kg^{-1}. The optimal TLA/FM could not be determined at Site 3 as there was not enough variability in TSS to create an inflexion point on the curve (Figures 3 and 4).

3.2. Dormant biomass distribution and vine balance ratios

Overall, cane mass, old cane mass and PM significantly increased with increasing node numbers at Site 1 ($p < 0.01$), but they did not change significantly over both seasons, although there was a clear trend toward higher mass on low-node vines in the second season (Table 7). On the contrary, the average cane mass and the average old cane mass significantly increased with decreasing node numbers ($p < 0.001$) except at Site 1 in 2019/2020, where the increase was not statistically significant. The patterns depicted at Site 1 regarding pruning mass (cane and old cane mass) as well as the average cane mass and old cane mass, were mirrored in the other two sites. For example, at Sites 2 and 3, the average cane mass on 10-node vines was more than twice that of 50-node vines, and at Site 2, the average cane mass varied within the same proportions (Table 7).

In 2019/2020 at Site 1, FM/CM and FM/PM increased with increasing node loads, with 10-node vines having FM/CM values at or below 3.5 kg kg^{-1} and FM/PM at or below 2.5 kg kg^{-1}. In 2020/2021, both FM/CM and FM/PM did not change significantly across node treatments but followed a trend of increasing values with increasing node numbers. At Site 2 and 3, FM/CM and FM/PM equally remained below 5.0 kg kg^{-1} despite low-node vines having significantly lower values than high-node vines (Table 8).

When the total bunch mass per vine (vine yield), TSS concentrations at harvest and the FM/PM or FM/CM were plotted against one another, no optimal ratios could be determined for harvest TSS (Figures S6 and S7). However, as FM/PM or FM/CM increased, total bunch mass increased while TSS decreased, although this was a weak relationship ($R^2 < 0.45$; Figures S6 and S7). However, ELA/FM and FM/PM or FM/CM were related (e.g., $R^2 = 0.69$ Site 3 season 2020/2021; Figures 5 and 6) where for example an ELA/FM of 0.75 m^2 kg^{-1} corresponded to an FM/CM and FM/PM of, respectively, 5.95 and 4.2 kg kg^{-1} for Site 1 season 2019/2020, 3.9 and 2.9 kg kg^{-1} for Site 1 in season 2020/2021, 4.0 and 3.0 kg kg^{-1} for Site 2 and 2.8 and 2.4 kg kg^{-1} for Site 3.

DISCUSSION

1. Grapevine response to node number during ripening

1.1. TSS accumulation and the source–sink relationship

Time to target TSS concentrations (21 °Brix) was delayed, and TSS concentrations at harvest reduced with increasing node numbers (Table 1; Figure 1; Table 2) which concurs with previous research on Sauvignon blanc (Greven *et al.*, 2015; Trought *et al.*, 2011) and other cultivars (Freeman *et al.*, 1980) where sugar accumulation was delayed as the node number increased. Previous studies on New Zealand Sauvignon blanc response to increasing node numbers attributed the low TSS accumulation and delayed ripeness observed on high-node vines to their high crop load

TABLE 7. Effect of increasing node load on pruning mass.

Cane node loads	Site 1 Season 2019/2020	Site 1 Season 2020/2021	*p-value**	Site 2 season 2020/2021	Site 3 Season 2020/2021
			Cane mass (kg)		
N10	0.67 ± 0.07 bc|A	0.89 ± 0.08 c|A	ns	1.21 ± 0.14 a	1.58 ± 0.13 a
N20	0.66 ± 0.07 c|B	0.94 ± 0.08 bc|A	< 0.05	1.06 ± 0.11 a	1.87 ± 0.07 a
N30	0.97 ± 0.11 ab|A	1.26 ± 0.11 ab|A	ns	1.02 ± 0.08 a	1.95 ± 0.10 a
N40	1.15 ± 0.11 a|A	1.32 ± 0.12 a|A	ns	1.17 ± 0.10 a	1.78 ± 0.13 a
N50	1.11 ± 0.11 a|A	1.24 ± 0.13 ab|A	ns	1.22 ± 0.12 a	1.74 ± 0.07 a
p-value	< 0.01	< 0.05		ns	ns
			Old cane mass (kg)		
N10	0.12 ± 0.01 d|A	0.17 ± 0.01 c|A	ns	0.16 ± 0.02 c	0.22 ± 0.07 d
N20	0.18 ± 0.01 d|B	0.23 ± 0.01 b|A	< 0.01	0.23 ± 0.01 bc	0.29 ± 0.01 cd
N30	0.29 ± 0.02 c|A	0.33 ± 0.01 a|A	ns	0.27 ± 0.02 b	0.36 ± 0.01 bc
N40	0.37 ± 0.02 b|B	0.35 ± 0.01 a|B	ns	0.34 ± 0.03 a	0.45 ± 0.02 ab
N50	0.47 ± 0.02 a|A	0.39 ± 0.03 a|A	ns	0.41 ± 0.02 a	0.48 ± 0.02 a
p-value	< 0.001	< 0.001		< 0.001	< 0.001
			Total pruning mass (cane mass + old cane mass) (kg)		
N10	0.80 ± 0.08 b|A	1.06 ± 0.09 b|A	ns	1.38 ± 0.16 a	1.85 ± 0.11 a
N20	0.84 ± 0.08 b|B	1.17 ± 0.08 b|A	< 0.01	1.28 ± 0.11 a	2.16 ± 0.08 a
N30	1.25 ± 0.12 a|A	1.59 ± 0.12 a|A	ns	1.28 ± 0.10 a	2.32 ± 0.10 a
N40	1.52 ± 0.13 a|A	1.69 ± 0.13 a|A	ns	1.51 ± 0.12 a	2.23 ± 0.14 a
N50	1.59 ± 0.14 a|A	1.63 ± 0.16 a|A	ns	1.63 ± 0.15 a	2.22 ± 0.09 a
p-value	< 0.001	< 0.001		ns	ns
			Average cane mass (g)		
N10	41.1 ± 4.2 a|A	52.4 ± 5.7 a|A	ns	69.2 ± 8.7 a	94.1 ± 11.1 a
N20	35.3 ± 5.3 ab|A	37.5 ± 3.9 b|A	ns	48.9 ± 6.1 b	79.6 ± 4.9 a
N30	36.0 ± 3.7 ab|A	42.4 ± 4.2 ab|A	ns	36.3 ± 3.6 bc	62.2 ± 3.9 b
N40	37.5 ± 4.4 ab|A	37.1 ± 3.4 b|A	ns	36.3 ± 4.8 bc	45.5 ± 3.6 bc
N50	30.5 ± 3.4 b|A	31.5 ± 3.6 b|A	ns	30.1 ± 3.9 c	40.4 ± 2.6 c
p-value	< 0.05	< 0.05		< 0.001	< 0.001
			Average old cane mass (g)		
N10	126.0 ± 11 a|B	167.3 ± 18 a|A	< 0.05	163.8 ± 21 a	160.0 ± 11 a
N20	90.6 ± 5.5 b|B	116.9 ± 7.3 b|A	< 0.01	112.6 ± 8.4 b	144.1 ± 8.2 a
N30	95.1 ± 7.4 b|A	110.6 ± 6.4 bc|A	ns	88.3.3 ± 7.7 c	120.8 ± 4.6 b
N40	91.7 ± 6.6 b|A	86.5 ± 4.7 bc|A	ns	85.3 ± 9.1 c	120.0 ± 5.6 b
N50	90.2 ± 7.2 b|A	98.1 ± 7.6 bc|A	ns	82.4 ± 6.9 c	113.0 ± 6.5 b
p-value	< 0.001	< 0.0001		< 0.001	< 0.0001

N10, N20, N30, N40 and N50 refer to the total node number on vine's canes equals 10, 20, 30, 40 and 50 nodes, respectively. Values are mean ± standard error of the mean of 15 vines for Site 1 and 10 vines for Sites 2 and 3. Means sharing the same lowercase letter in a column (cane node load comparison) or the same uppercase letter in a row (seasons comparison at Site 1) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$). * *p-value* indicates the level of significance of the variable measured at Site 1 between the first and second season.

TABLE 8. Effect of increasing node load on indicators of vine balance—Fruit mass: cane mass ratio (FM/CM) and Fruit mass: pruning mass ratio (FM/PM).

Cane node load	Site 1 season 2019/2020	Site 1 season 2020/2021	*p-value**	Site 2 season 2020/2021	Site 3 season 2020/2021
			Fruit Mass to Cane Mass ratio—FM/CM (kg kg^{-1})		
N10	3.35 ± 0.7 c | A	2.21 ± 0.3 a | B	ns	1.31 ± 0.2 d	1.06 ± 0.1 c
N20	5.54 ± 0.8 bc | A	3.46 ± 0.4 a | B	< 0.05	2.37 ± 0.3 cd	1.83 ± 0.2 b
N30	5.32 ± 0.8 bc | A	2.65 ± 0.3 a | B	< 0.01	3.14 ± 0.3 bc	2.35 ± 0.2 b
N40	5.80 ± 0.8 ab | A	3.20 ± 0.4 a | B	< 0.01	3.65 ± 0.4 ab	3.45 ± 0.3 a
N50	7.74 ± 0.9 a | A	3.72 ± 0.5 a | B	< 0.001	4.34 ± 0.4 a	3.33 ± 0.2 a
p-value	< 0.01	ns		< 0.001	< 0.001
			Fruit Mass to Pruning Mass ratio—FM/PM (kg kg^{-1})		
N10	2.60 ± 0.5 c | A	1.71 ± 0.2 a | A	ns	1.15 ± 0.1 c	0.90 ± 0.0 c
N20	4.08 ± 0.5 ab | A	2.57 ± 0.2 a | B	< 0.05	1.90 ± 0.2 bc	1.58 ± 0.1 b
N30	3.84 ± 0.4 bc | A	2.02 ± 0.2 a | B	< 0.01	2.45 ± 0.2 ab	1.96 ± 0.1 b
N40	4.19 ± 0.5 ab | A	2.32 ± 0.3 a | B	< 0.01	2.79 ± 0.3 a	2.71 ± 0.2 a
N50	5.31 ± 0.5 a | A	2.71 ± 0.3 a | B	< 0.001	3.19 ± 0.3 a	2.60 ± 0.1 a
p-value	< 0.01	ns		< 0.001	< 0.001

N10, N20, N30, N40 and N50 refer to the total node number on vines' canes equals 10, 20, 30, 40 and 50 nodes, respectively. Values are mean ± standard error of the mean of 15 vines for Site 1 and 10 vines for Sites 2 and 3. Means sharing the same lowercase letter in a column (cane node load comparison) or the same uppercase letter in a row (seasons comparison at Site 1) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$). * *p-value* indicates the level of significance of the variable measured at Site 1 between the first and second season.

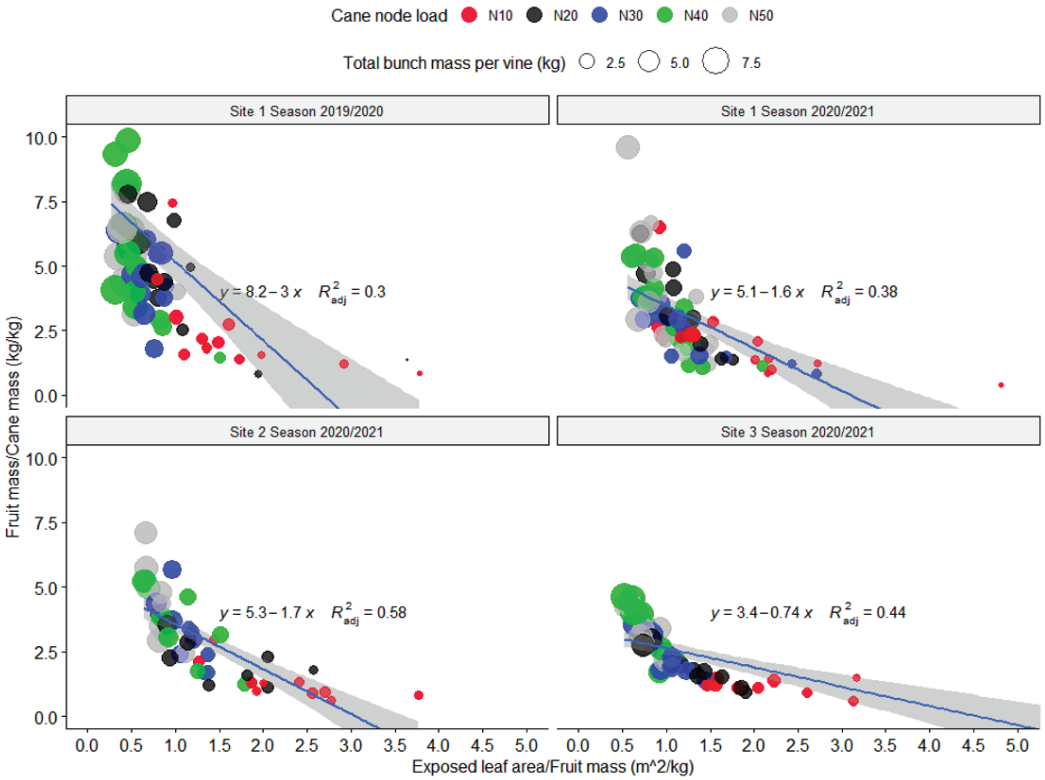


FIGURE 5. Relationship between total bunch mass per vine, node load, fruit mass–cane mass ratio (FM/CM) and exposed leaf area-fruit mass ratio (ELA/FM).

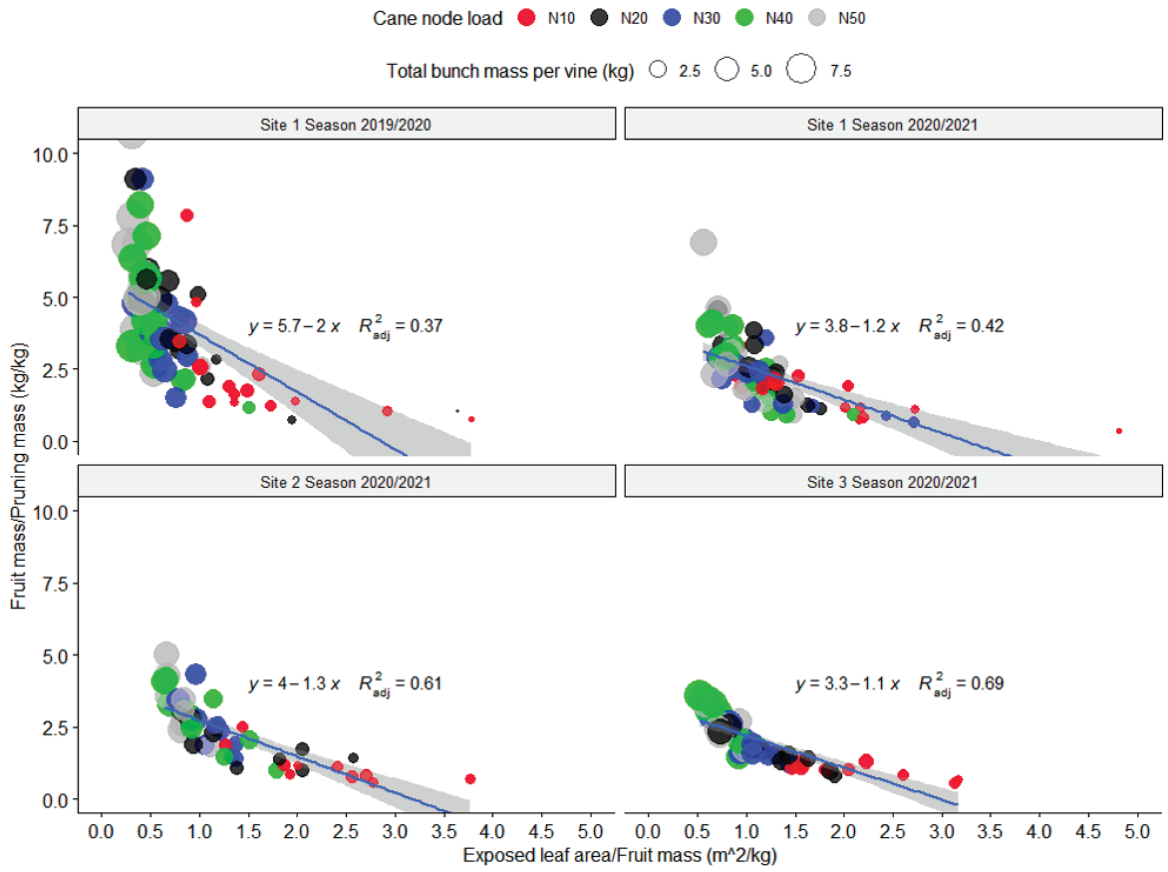


FIGURE 6. Relationship between total bunch mass, node load, fruit mass–pruning mass ratio (FM/PM) and exposed leaf area-fruit mass ratio (ELA/FM)

(i.e., the amount of fruit bore by the vine) but not to the source–sink ratio as leaf area was not quantified (Greven *et al*., 2014; Greven *et al*., 2015). In the present study, the source size was measured through TLA and exposed area ELA.

The high TSS concentrations measured on 10-node vines were directly related to their high source–sink ratio (Figures 3 and 4). With a significantly much larger TLA/FM and ELA/FM (Table 6), low-node vines potentially supplied more photosynthates to the developing berries. Studies on source–sink manipulations show that leaf removal and shoot trimming (source restriction) for a given crop size are accompanied by a decrease in berry TSS concentrations whereas for a given leaf area, fruit thinning (sink restriction) results in high sugar concentrations (Bravdo *et al*., 1985; Etchebarne *et al*., 2010; Keller, 2015; Parker *et al*., 2015; Parker *et al*., 2016; Poni *et al*., 2006; Poni *et al*., 2009; Santesteban and Royo, 2006). Therefore, as the source size (leaf area) gets larger relative to the sink size, the TSS concentration and accumulation rate rise up to a maximum and then plateaus. Because they had a much larger leaf area for an equivalent amount of fruit, 10-node vines achieved much higher TSS concentrations than 50-node vines. Kliewer and Dokoozlian (2005) found that on vines trained to single-canopy systems, a total leaf area to fruit mass ratio of 0.8–1.2 m^2 kg^{-1} was necessary to achieve optimum TSS concentrations. In the present study, an ELA/FM and TLA/FM of 0.75 and 2.0 m^2 kg^{-1}, respectively, were necessary for optimum berry ripening (TSS accumulation), other factors being equal. Interestingly, these values were similar across all three sites with the only exception of Site 3, where the critical TLA/FM could not be determined because the variability in TSS was not high enough to create an inflexion point on the curve (Figure 4d). Source–sink ratio values for optimal TSS are particularly useful in guiding in-season canopy management practices such as leaf removal as well as crop load management practices such as inflorescence and fruit thinning.

The general rule of a leaf area to fruit mass ratio of 0.8–1.2 m^2 kg^{-1} corresponding to a yield to pruning mass ratio of 5–10 kg kg^{-1} (Kliewer and Dokoozlian, 2005; Kliewer and Weaver, 1971) was not supported by our data. The authors compared several varieties not including Sauvignon blanc. Site properties, climate, training and pruning systems were different from those encountered and practised in New Zealand. Moreover, there was only a weak linear relationship between TSS and FM/PM or FM/CM, suggesting that both metrics do not have a strong linear relationship (Figures S6 and S7). Nevertheless, based on these weak linear relationships, an ELA/FM of 0.75 m^2 kg^{-1} corresponded to 3.0–6.0 kg kg^{-1} FM/CM and 2.5–4.5 kg kg^{-1} FM/PM. The wide range of these values was a clear indication that

ratios are site, variety, management and season-dependent. Overall, the FM/CM and FM/PM of source-sufficient vines (N10 vines) were at the lower end or below the range of 3.0–5.0 and 2.0–4.0 kg kg^{-1}, respectively, whereas that of source-restricted vines (N50 vines) was at the upper end or above those ranges. FM/CM and FM/PM values at the lower end of the range were an indication of high vigour and high capacity (total cane mass or pruning mass and fruit mass) suggesting that at pruning, the node number of such vines must be raised to meet their capacities. On the contrary, values at the upper end of the range signalled low vine vigour and reduced capacity and consequently decreased node load at pruning.

Greven *et al*. (2015) noted that throughout four growing seasons, vines pruned to high node numbers accumulated TSS at slower rates in the first two seasons and then progressively reached the same TSS accumulation rate as low node vines by the fourth season. In the second harvest at Site 1, N10 and N50 vines reached comparable TSS concentrations, and this could be interpreted as early signs of these vines reaching the stability observed by Greven *et al*. (2015). This assumption was considered with care for the following reasons: (1) Greven *et al*. (2014) did not notice a sharp yield drop across their node treatments the second season as in this trial but rather a moderate and gradual yield rise on low node vines and a gradual yield drop on high node vines; (2) low- and high-node vines in Greven *et al*. (2015) reached comparable TSS accumulation gradually throughout several seasons and not as abruptly as in the second season in this trial. Therefore, the comparable TSS concentrations observed in this study were mainly driven by the sharp yield drop in the second season. Possible reasons for this yield drop are discussed below. Finally, as the results presented here were only collected over two growing seasons, it was too early to assume any stabilisation of the TSS accumulation rates between the high-node and low-node vines.

1.2. TA and pH response to retained node numbers

Grape TA and pH values were not affected by varying node loads, which is consistent with earlier research on other grapevine cultivars such as Concord, Seyval and Chambourcin grapevines (Dami *et al*., 2005; Edson *et al*., 1995; Keller *et al*., 2004). Trought *et al*. (2011) also observed that in two seasons out of three, pH did not change when Sauvignon blanc was pruned from 20 to 40 nodes. Even when the source–sink ratio is altered either with leaf removal or fruit thinning, pH and TA remain similar, confirming the assumption that these two maturity variables are independent of the photosynthesis rate (Parker *et al*., 2015; Parker *et al*., 2016) as well as of the source–sink ratio. The null effect of node load on pH and TA concentration is an indication that these properties are influenced by other factors such as soil physicochemical properties, solute transport, bunch microclimate (temperature), water and mineral nutrition (Conradie and Saayman, 1989; Kliewer, 1973; Pereira *et al*., 2006; Spayd *et al*., 1987) rather than node load. Under some circumstances, however, strong vegetative growth together with the development of a dense canopy may increase shading, resulting in high TA concentrations, as was noted on 10-node vines at Site 1 (Keller and Koblet, 1995; Keller *et al*., 1998).

2. Yield formation and relation with yield components

Grapevine yield was greatly affected by the change in node load. A very strong linear yield increase with increasing node numbers was observed across all sites and seasons (Figure S2), confirming previous findings on Sauvignon blanc and other grapevine cultivars (Archer and Fouche, 1987; Greven *et al*., 2014; Jackson *et al*., 1984; Kurtural *et al*., 2006). At the scale of the whole vine, the yield increase was mainly driven by the number of grape bunches, reflecting the higher number of count nodes retained at pruning and that of count shoots that emerged later (Figure 2; Table 5). The average bunch mass and bunch mass per shoot seemed to be insensitive to node treatments at Site 1 over two seasons and at Site 2 and Site 3 in the first season of node treatments. These results partially agree with those of Greven *et al*. (2014) and Jackson *et al*. (1984) who also found that the average bunch mass per vine did not change during the first and second seasons of node treatments. Similar results were equally observed on Shiraz vines pruned to 20 and 40 nodes under non-irrigated conditions (Freeman *et al*., 1979). However, in the context of the quality evaluation of cane pruning decisions made by an automated pruning system, or by human pruners, a more detailed analysis is required to determine the performances of the retained canes regarding yield components (Epee *et al*., 2022a).

The canes of 10-node vines performed better (higher yield components) than canes of 50-node vines, particularly in the second season of node treatment (Tables 4 and 5). The average bunch mass, bunch mass per shoot, and bunch number per shoot were significantly higher on canes of low-node vines compared with those of high-node vines (Tables 4 and 5). This could be ascribed to the selection of more fruitful canes, characterised by a thicker diameter and a higher average cane mass (Eltom *et al*., 2014; Jones *et al*., 2013; Sommer *et al*., 2000). As already discussed in Epee *et al*. (2022a), the pruner had more options in selecting thicker and heavier canes to form retained canes and spurs on N10 and N20 vines than on N50 vines, which generally had thinner, lighter and, thus, potentially less fruitful canes (Table 7). In the first season of node treatments, however, the performances (yield components) of the canes selected in winter were not significantly different across the five node treatments (Tables 4 and 5). This is because, in the first season of node treatments, all vines were at the same physiological status (i.e., overwintering carbohydrate reserves, inflorescence initiation, average cane mass) as they have all been pruned to the same node number (36 nodes on canes). The pruner selected canes from a pool of dormant shoots having similar fruitfulness, and this resulted in harvest in similar average bunch mass, bunch mass per shoot and bunch number per shoot on canes across all five node treatments (Tables 4 and 5).

Shoots on canes and spurs outperformed (higher yield components) those on the vine head regardless of node load (Table 3 to Table 5). Shoots on the vine head developed either from basal buds of canes removed the previous winter or from latent buds hidden in the old wood. In the literature, latent buds and basal buds are generally considered sterile or unfruitful, i.e., they do not contain inflorescence primordia and thus never develop into fruit-bearing shoots (Galet, 2000). Although some earlier studies have found that latent buds are as fruitful as buds on retained canes (Huglin and Julliard, 1955), in this study, buds on the vine head (latent and/or basal buds) were neither sterile—as they bore some grape bunches—nor as fruitful as retained buds on canes and spurs as they bore fewer bunches. Consequently, Sauvignon blanc head buds could be better described as being less fruitful or of very low fruitfulness but not as being completely unfruitful or sterile, at least at the sites where the experiments were conducted.

Between 2019/2020 and 2020/2021, a significant yield reduction occurred at Site 1 on all node treatments. This yield reduction was also noted across most New Zealand wine-grape growing regions (New Zealand Wine, 2021). The drop was mainly driven by the decrease in the average bunch mass and the bunch mass per shoot (Figure 2). Grapevine yield is determined over two seasons and is greatly influenced by weather conditions—mainly temperature and rainfall—at two critical developmental stages: inflorescence initiation in the previous season (season 1) and flowering in the current season (Buttrose, 1974; Trought, 2005; Vasconcelos *et al*., 2009; Zhu *et al*., 2020), but also by the size and mass of canes selected at pruning (Eltom *et al*., 2014; Jones *et al*., 2013; Sommer *et al*., 2000). It is not clear from our data what might have caused this general yield drop. However, the cooler temperatures at fruitset in November 2020 (average air temperature of 14.0 °C in November 2020 compared with 15.9 °C in 2019) could have played a crucial role (Figure S1, Table S2) given that significant shift from ideal flowering and fruitset conditions (air temperature 20–30 °C) can have a great impact on vine yield (Currle *et al*., 1983; Dunn and Martin, 2000; Eltom *et al*., 2014; Petrie and Clingeleffer, 2005; Trought, 2005; Vasconcelos *et al*., 2009; Zhu *et al*., 2020). Since cane fruitfulness is dependent on thickness and mass (Eltom *et al*., 2014; Jones *et al*., 2013; Sommer *et al*., 2000), it is also possible that high-node vines, which had the highest yield drop together the lowest average cane mass, have been impacted more because the canes retained already had a potentially lower fruitfulness (low average cane mass). Furthermore, these vines might have been lower in carbohydrate reserves (low average old cane mass) to buffer the adverse weather compared with low node vines which were higher in carbohydrate reserves (high average old cane mass).

3. Berry size and the source–sink relationship

Previous research on Sauvignon blanc and other grapevine cultivars has shown that berry mass is very sensitive to any manipulation of the source–sink ratio either through defoliation, shoot trimming, crop thinning or node numbers (Dunlevy et al., 2013; Eltom et al., 2014; Freeman et al., 1979; Greven et al., 2014; Parker et al., 2015). In the current study, despite their high source–sink ratio, the berry mass on low-node vines was not significantly different to that of high-node vines (Figure 1) which disagrees with Greven et al. (2014) who found that Sauvignon blanc berry mass decreased with increasing node numbers in two out of four seasons. Under source-limiting conditions, grapevines can remobilise carbohydrate reserves stored in permanent and semi-permanent vine structures to compensate for the limited supply of photosynthates from leaves (Holzapfel *et al*., 2010; Zufferey *et al*., 2012). This remobilisation is possible because, during ripening, berries become strong sinks (Buttrose, 1966; Hale and Weaver, 1962; Wardlaw, 1990). Greven *et al*. (2014) investigated the effects of node load on young vines (3-year-old) with potentially limited carbohydrate reserves and consequently, the compensatory effect of remobilisation could not offset the limited supply of carbohydrates from leaves. In the current study mature grapevines aged over 10 years old were used and although root and trunk carbohydrates were not measured, it was very likely that these vines had greater potential for remobilisation to offset the restricted source size, resulting in comparable berry mass across all node loads. Additionally, the source restriction induced by the highest node number (50 nodes) might have been less strong than in Greven *et al*. (2014) to be overcome by remobilisation. Results of this research indicate that the berry mass of mature grapevines is less sensitive to the manipulation of the source–sink ratio within the range of 10 to 50 retained nodes. However, additional research will be needed to understand the extent of the remobilisation buffering capacity over time (three to four years) and as the node range increases to 72 nodes or higher.

Even under extreme sink-limiting conditions, once grape berries have reached their maximum size, their sink strength diminishes, and the excess photosynthates are stored in the permanent vine organs (Keller, 2015). In other words, despite an abundant supply of carbohydrates, berry mass and size reach a maximum, restricted by the extensibility of berry skin and epidermal cells (Matthews *et al*., 1987; Staudt *et al*., 1986). Interestingly, low-node vines had the heaviest average cane mass and old cane mass, which suggests that sufficient carbohydrate was available to cater for adequate berry and bunch growth (including the highest TSS concentration) while the excess carbohydrate was stored in permanent and semi-permanent vine parts (Table 7). Therefore, due to their larger source–sink ratio, low-node vines bore significantly heavier grape bunches and a higher number of bunches on a per cane basis compared with high-node vines despite having comparable berry mass (Tables 3 and 4, Figure 1).

However, previous research shows that source limitation (by defoliation shortly after flowering) is associated with reductions in the number of inflorescences, inflorescence primary branches, flowers per inflorescence and berry number per grape bunch the following season (Bennett *et al*., 2005). Therefore, as this research suggests, a source restriction

imposed by retaining high node numbers seems to affect less the final berry size but more the final TSS as well as carbohydrate storage in permanent and semi-permanent vine parts.

CONCLUSION

The objective of this research was to investigate how mature vines respond to increasing node loads. Retaining higher node numbers resulted in (1) higher yields driven by a greater number of smaller grape bunches; (2) lower TSS concentrations and accumulation rate due to a reduced source–sink ratio; (3) comparable TA concentrations, pH and berry mass with low-node vines; (4) lighter canes and old canes as a result of greater carbohydrate remobilisation and restricted carbohydrate storage despite an overall greater pruning mass; (5) vine balance ratios above 3.0–5.0 kg kg^{-1} for FM/CM and 2.0–4.0 kg kg^{-1} for FM/PM and below 1.0–1.5 m^2 kg^{-1} for ELA/FM for the vineyard sites of this study.

For an optimal berry ripening (TSS), an ELA/FM and TLA/FM of 0.75 and 2.0 m^2 kg^{-1}, respectively, was necessary and corresponded to FM/CM and FM/PM 3.0–6.0 kg kg^{-1} and 2.5–4.5 kg kg^{-1}, respectively. The variability in yield over the two seasons of this experiment highlighted the importance of two complementary management techniques: retained node number at winter pruning and source–sink adjustments later in the season. A low source–sink ratio induced by a high node load not only reduced the vine capacity to fully ripen the current crop but also jeopardised the next season's reproductive potential. Consequently, Sauvignon blanc Ravaz index (FM/CM or FM/PM) should be used in winter to set the vine node number but also closely monitored in-season with the optimal source–sink values (ELA/FM or TLA/FM) to ensure adequate TSS accumulation and sufficient carbohydrate storage before leaf fall. The FM/CM and FM/PM ratios could be used retrospectively to evaluate human pruning decisions on the grapevine vegetative and reproductive growth over the past season and prospectively to inform on the appropriate pruning level (retained node number). The optimal ELA/FM and TLA/FM could be used to inform the quantity of fruit to drop during inflorescence or fruit thinning to achieve optimal fruit ripening.

In the first season of node treatments, the performances of canes (i.e., average bunch mass, bunch number per shoot and bunch mass per shoot) were comparable across node treatments because they were selected from a pool of canes having similar potential fruitfulness and vigour (cane mass). In the second season, however, the performances of canes on low-node vines became superior to those of high-node vines, likely because their node load was above their capacity, and they were source-restricted (low source–sink ratio). This resulted in high vigour shoots (high average cane mass and diameter) and greater fruitfulness.

Head shoots had the lowest performance (yield components) because they originated from the numerous latent buds and/or basal buds on the vine head and were of very low fruitfulness but not completely sterile or unfruitful. Cane shoots were more fruitful and productive than spur shoots, demonstrating the relatively lower fruitfulness of lower nodes (position 1–3 from the origin) compared to higher node positions.

Carbohydrate reserves play a central role in the grapevine response to retained node numbers. Because stored carbohydrates were not directly measured, additional research will be needed to understand the extent of the remobilisation buffering capacity of mature grapevines over a longer period (three to four years) and at a very high node number. Additionally, research will be needed to quantify the balance of carbohydrate reserves at the start and end of the growing season, given that a high node number seems to deplete them, and a low node number replenishes them.

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